Machiavellian Intelligence retrospective

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Machiavellian Intelligence is a label - or perhaps banner headline would be more accurate - coined for the hypothesis that a major contribution to the evolution of intelligent behavior, in the human lineage and perhaps also more generally among animal groups, has been the adaptive challenge of dealing with the complexities of living in a social group (Byrne & Whiten, 1988). An individual's success involves striking a balance between cooperation and competition with a range of diverse other individuals, requiring subtle social skills rather than brute power.

Today, the potential importance of social complexity driving the evolution of intelligence is widely acknowledged: but that has not always been so. Before the 1980s, it was generally accepted that intelligence, in the sense of that package of useful skills that impress people as being in some way "smart", evolved to deal with the physical challenges of the environment: finding and getting access to food, remembering safe places, noticing signs of danger, etc. For human evolution, a special form of this hypothesis was labeled "Man the tool maker" (Oakley, 1949). Complex societies were considered a by-product of this technical intelligence.

Radically different views were occasionally expressed, pointing instead to the problems set by social living. Michael Chance and Allan Mead (1953), impressed with the social maneuvering of male baboons, suggested that social challenges might select for greater intelligence in general. Alison Jolly (1966), pioneering the study of highly-social lemur species whose members seemed technically inept, suggested reversing the common view of primate society as a product of intelligence, postulating instead that general intelligence might result from the complexity of social living. The psychologist Nicholas Humphrey (1976) was familiar with the impressive skills captive monkeys displayed in dealing with experimenters' gadgetry, but he could see nothing remotely as challenging in their natural environment. He made a strong case that they met greater problems simply by living socially, and proposed that general intelligence had evolved as an adaptation to specifically to group living, itself driven by other factors such as reduction of predation risk. Andrew Whiten and I argued that these ideas deserved serious consideration, and put together a book which reprinted those seminal theory papers plus a range of current studies that gave support to the hypothesis, which we labelled "Machiavellian Intelligence" (MI) and used as the book's title (Byrne & Whiten, 1988). Thirty years on from the book's publication, in this essay I will offer a personal reflection on how the ideas in it have influenced understanding of the evolution of intelligence, how they have been tested (and sometimes misunderstood), and whether they are still relevant.

The apposite nature of Niccolo Machiavelli's maxims to describe the social maneuverings of non-human primates had first been pointed out by Frans de Waal, who chose Machiavelli quotations to explain the logic of chimpanzees' "political" decisions about social alliances (de Waal, 1982). In giving advice to an aspiring prince, Machiavelli (1532/1979) stressed the importance of being friendly, cooperative, kind and generous – just until it paid not to be so. Similarly, the MI hypothesis applies just as much to the social sophistication shown in friendship formation, reconciliation, coalitions and alliances, kin support and reciprocal altruism, as it does to deception and overtly political manipulation. Old World monkeys, for instance, use grooming to build up relationships with unrelated individuals who later come to their aid in conflicts (Dunbar, 1991); if important monkey friendships are disrupted by a fight, one of the combatants will soon make friendly overtures which usually result in repairing the relationship (Cords, 1992); if a monkey's relative or ally is attacked by a

high-ranker, then they may still respond by attacking a lower-ranking relative of the attacker, in a sort of monkey vendetta (Seyfarth & Cheney, 1984). Individuals sometimes use deception tactically, such as when a young monkey, frustrated by seeing an adult monopolizing a good food source, gives a scream that cause his (higher-ranking) mother to rush to his aid and displace the other monkey: "coincidentally" leaving the food source for the youngster to monopolize (Byrne & Whiten, 1985; Whiten & Byrne, 1988) see also (Kean et al., 2017; Wheeler, 2009; Wheeler, Tiddi, & Heistermann, 2014). All this implies a great deal of social knowledge, about who's a friend or relative of whom, and that knowledge is often acquired indirectly, by "eavesdropping" on conflicts among third-parties, as has been shown by simulating conflicts with artfully-constructed sequences of monkey calls (Kitchen, Cheney, & Seyfarth, 2005). The ultimate benefits are selfish; the proximate means may be altruistic, or not. MI should therefore not be conflated – though it sometimes has been – with the human personality trait of "Machiavellianism" (Christie & Geis, 1970), which refers specifically to an ability to detach from conventional morality and emotionality in order better to deceive and manipulate other people. MI is not about morality, and not restricted to "nasty" actions. Using the synonym "social intelligence" does avoid such confusion, but brings in turn the risk of missing the importance of selfish benefit to the agent or its kin in MI – unlike the case of "prosocial" actions (Jensen, 2016) – which would be equally misleading.

There is no doubt that MI gave impetus to the great burgeoning of studies on animal social complexity and maneuvering over the last 30 years, and it became a popular explanation for the evolutionary origins of intelligence. Clear evidence in support of that position has been more elusive. Part of the difficulty with testing the MI hypothesis relates to ambiguities of its scope (Byrne, 1996a; Whiten, 1997). Is MI required to be the primary driver of cognitive advance, and therefore refuted by any clear cases where it is not? If, instead, MI is just one of many factors that may select for intelligence, interpreting findings is more problematic. Is MI supposed to select for a specific 'module' of advanced social intelligence, contrasting with primitive abilities in other domains? If, instead, the result is going to be general intellectual advance, then tying it back to a social origin is much more difficult: how can we be sure which arena was the evolutionary driver of intelligence that is manifest in many correlated ways? Separating "arenas of expertise" is itself tricky: if acquiring a valuable feeding skill is aided by observational learning from a companion, is that a social or a physical aptitude? At its most general, MI must surely predict that any highly-social species should be more intelligent than an asocial one, other things being equal: but when are they equal? If the relatively solitary orangutan consistently outperforms the obligate social baboon, does that refute the MI hypothesis because both are primates – or not, because one is an ape and the other a monkey? In every one of these cases, over the last 30 years different authors have made opposite choices, and exploring the consequences of each is well beyond the scope of this essay: the point is rather that no simple "right/wrong" answer is to be expected.

The long history of trying to measure differences of intelligence among animal species gives little confidence that even clear formulations can be tested against reliable behavioral data (Macphail, 1985). Researchers therefore turned to brain size as a proxy measure of intelligence; but this approach also has its problems. Like many biological parameters, brain size increases with body size; the relationship is generally curvilinear within a set of related species, so plotting on logarithmic coordinates has been used to produce a straight line (allometric scaling). Larger or smaller brain sizes than expected are deduced from (1) the intercept with the Y-axis, compared with that of other taxonomic groups plotted; and (2) deviations from the averaged line of a single taxonomic group under examination. As if this were a sort of IQ test, the ratio of observed to expected brain size - the "encephalization quotient" EQ - has sometimes been treated as species intelligence, on the assumption that the brain is in some way an "on-board computer" and bigger is better. Scaling

against body size, it appears that it is diet complexity – among primates, frugivory rather than folivory – that correlates with brain enlargement, rather than any measure of social complexity (Clutton-Brock & Harvey, 1980; DeCasien, Williams, & Higham, 2017). However, experience with man-made systems suggests that the upper limit of computing power is given by the *absolute* number of components, rather than brain size *relative* to body size. In consequence, two species with identical EQs but different body sizes can vary hugely in the number of extra neurons they possess, above or below that predicted from their body size. Rather than giving a direct indication of intelligence, EQ instead measures cost (Byrne, 1996b). The brain is a metabolically expensive organ and requires energy remorselessly at normal ambient temperatures (Aiello & Wheeler, 1995), so the larger the brain the higher the risk to an animal. Larger-bodied species can "afford" larger brains, since their basal metabolic rate will in general be higher (though note that non-human primates have unusually low metabolic expenditure among placental mammals, affording brain size increase without change in body size or metabolic acceleration (Pontzer et al., 2014)), but any species with a brain larger-than-expected from its body (i.e. high EQ) must have been under selection for brain size increase; those species with low EQ have been able to manage with smaller brains and thus reduce their costs. Powerful selection for larger or smaller brains certainly gives a clue about the need for cognition, but potential intellectual power is better measured by absolute number of computing components and connections between them.

For species that live long-term in stable social groups, the average size of social groups is typically used as a rough-and-ready index of the social complexity confronting any individual (Dunbar, 1992; Shultz & Dunbar, 2007). Numerous studies on a range of mammalian taxa have found positive correlations between absolute brain size (or absolute size of the neocortex; or the ratio of neocortex size to the rest of the brain) and average group size, which are taken to support the MI hypothesis (Barton & Dunbar, 1997). Much of the early work was carried out on primates, whose groupings are typically long-lasting, and in which researchers have shown that relationships are differentiated: an individual knows others as individuals, and behaves quite differently towards them according to their kin relationships, friendships, and history of part interactions with them. These characteristics are critical for the MI hypothesis, because it is only when relationships are differentiated among individuals that there is any real possibility of social complexity (Bergman & Beehner, 2015). Many groupings of mammals and birds are temporary aggregations, such as a winter flock of sparrows and finches foraging near a grain store, or a herd of deer or antelope feeding on a flush of young grass. Their typical group size is not predicted by MI to relate to any measures of brain size, and indeed they do not (Dunbar & Shultz, 2007; Emery & Clayton, 2005). Only for primates, and for some other mammalian families which live in semi-permanent groups, such as cetaceans and chiropteran bats, correlations with absolute brain size measures have regularly been found (Barton & Dunbar, 1997; Connor, 2007; Dunbar, 1993; Dunbar & Shultz, 2007; Holekamp, Sakai, & Lundrigan, 2007; Marino, 1996) but see Powell, Isler & Barton, 2017). Moreover, many brain functions do not contribute to the package of abilities we recognize as intelligence, but rather regulate the somatic and sensory functioning of the body; neither the brain, nor any specific brain part, is a dedicated 'thinking machine', and we have no principled way of taking account of all the other demands on neural capacity in addition to any cognitive computing. The idea that social complexity is a powerful driver of selection for cognitive power in animals is consistent with the social sophistication and manipulative tactics that have been increasingly documented among group-living animals in the last 50 years, but direct testing of the MI hypothesis will require good measures of intelligence that can be applied across species, and clearer statements of what exactly MI and competitor hypotheses predict, both of which have been lacking.

At the heart of the MI hypothesis lies the idea of behavioral complexity, another parameter that is not easy to measure (Byrne, Corp, & Byrne, 2001a; Cochet & Byrne, 2014; Sambrook & Whiten, 1997). Traits accepted as indicating social complexity among primates, and increasingly discovered in other taxonomic groups, include: third parties having an important role in deciding the outcome of conflicts, and in general the need to take account of 'triadic' relationships rather than simple dyadic ones; acquisition of rank by kin support; the use of grooming to cultivate 'friendships' with potentially useful individuals, friendships that persist over long time-scales and predict the distribution of mutual help; the repair of these relationships by targeted reconciliation after conflict; and informed choice of potential allies on the basis of individual characteristics. These traits are generally species-typical, so likely to be strongly channeled genetically. What might be minimally necessary, to benefit from such "hard-wired" traits? Individuals must possess certain fundamental cognitive capacities: (1) distinguish conspecific group members as individuals, and thus be able to respond differently to kin, (2) remember relative ranks and past affiliations, and (3) remember the personal histories of help given and received from various others (Byrne, 2016). Manipulation by tactical deception is reported only among certain individuals and varies in precise form even within a species, making genetical explanations improbable. Instead, most records of deception can be explained as learning from natural coincidences, provided individuals first possess a rich data-base of social knowledge and can learn new tactics over only a very few trials (Byrne, 1997b). Thus, most social complexity among animals can be underpinned simply by good skills of memory and perception, allowing rapid learning of nuanced distinctions among social companions. In support of the MI hypothesis, a strong case can be made that quantitative variation in perceptual, learning and memory abilities matches the challenge of living long-term in groups whose members distinguish each other as individuals. In the main, that case is based on cross-species analysis, but Ashton et al (2018) showed that individual differences in learning ability of Australian magpies (*Cracticus tibicen*) correlated with the size of their social groups, and even with their reproductive success.

Conspicuously absent in this account is any need for an individual to be able to represent and compute with what is going on in the mind of a competitor or an ally. Evidence that such mentalizing or "theory of mind" understanding is found in animals has been controversial, but is now becoming accepted for a few animal species, including all great apes (Call & Tomasello, 2008; Krupenye, Kano, Hirata, Call, & Tomasello, 2016) and some corvid and psittacine birds (Dally, Emery, & Clayton, 2010; Emery & Clayton, 2004), and possibly also toothed whales and elephants (Byrne, 2016). Can this distribution of species be explained by the MI hypothesis? Using the rough-and-ready metric of the average size of semi-permanent groups, great apes are simply not confronting greater social challenge than many monkey species, several of whom live in larger groups than any ape. Similarly, corvids and parrots do not live in particularly large groups: monogamous pairs are typically the largest long-term associations among birds, and those few species living in larger groups, often cooperative breeders, seem in any case to have smaller brains (Fedorova, Evans, & Byrne, 2017). The MI hypothesis therefore fails to predict the distribution of mentalizing ability across animal species (Byrne, 1997a), when the rough-and-ready index of semi-permanent group size is used to index complexity. Potentially salvaging the hypothesis for these awkward species, it has been argued that individuals in fission-fusion societies confront a significantly greater challenge of social complexity than indicated merely by the size of grouping with whom they show differentiated relationships (Amici, Aureli, & Call, 2008, 2010; Aureli et al., 2008). Certainly, chimpanzees, elephants and dolphins do live in such groups, and have little else obvious in common; but for other species the fit is less good. Spider monkeys are always found in fission-fusion social organization, yet have shown no sign of mentalizing ability; gorillas are usually found in cohesive groups, yet appear typical great apes in their mental representations. As Bergman and Beehner (2015) note, there is risk when retro-

fitting a hypothesis to known data; *a priori*, it might as easily be argued that it is in highly cohesive groups where the greatest payoff from representing other minds is to be gained.

Comparing the great apes with other primates, what stands out is not their social group sizes but their technical skills, whether expressed in tool-use or in other means of efficient food acquisition and preparation (Byrne, 1997a, 2005). The abilities of various crow species in using tools and solving mechanical puzzles suggests a similar case may be made for corvids (Bird & Emery, 2009; Seed, Emery, & Clayton, 2009). Apes are able to learn multi-step, hierarchically-organized programs of motor behavior, in which the two hands, and the separate fingers of the hands play independent by coordinated roles (Byrne & Byrne, 1993; Byrne, Corp, & Byrne, 2001b). I have argued elsewhere that the key to this package of abilities is the ability to parse observed behavior to expose its organization, and thus to learn by imitating the program-level of action (Byrne, 2003; Byrne, Hobaiter, & Klailova, 2011). This results in a rough-and-ready sort of understanding, based on the statistical properties of observed behavior, that enables apes also to understand social action and pass non-verbal theory of mind tasks – but in terms of behavioral organization and its results, rather than the full theory of mind understanding found in adult humans, which is dependent on propositional representation (Byrne, 2006, 2016).

So, have the ideas of MI had their day? Certainly, if it were ever imagined that MI would provide a complete explanation for the evolutionary origin of variation in intelligence among animals, such a hope is no longer tenable. Learning and problem-solving abilities vary even among animals that are in no significant way social – though see (Macphail, 1985) for a contrary view – and among social primates the differences between monkey and ape abilities do not accord with the predictions of MI. That is not to say that the challenge of living long-term in a group of associates who know each other as individuals, competing and collaborating with each other, has been shown to be trivial or irrelevant. Rather, the problem has been in testing its power in comparison to other factors, given the intricate interweaving of social and technical abilities, perceptual and motor aspects of cognition, life history strategy and metabolic constraints on brain sizes. Prophesying which approaches will lead to future breakthroughs is always a matter of guesswork, but if I had to make a guess, I would suggest that a reliable method of measuring cognitive challenge, one that was applicable to problem-solving in different domains, would most effectively remove obstacles to progress; for an early effort to develop such a metric, see (Byrne, 1993).

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